

THE RESPONSE OF GALL-INDUCING SCALE INSECTS (HEMIPTERA: ERIOCOCCIDAE: *APIOMORPHA* RÜBSAAMEN) TO THE FIRE HISTORY OF MALLEE EUCALYPTS IN DANGGALI CONSERVATION PARK, SOUTH AUSTRALIA

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Summary

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Mallee communities, especially the plant components, are often considered to be fire-adapted but there is no information on how effectively any phytophagous insects re-establish their populations after a wildfire. We addressed this issue by studying the scale insect genus *Apiomorpha* Rübssamen, in which species induce conspicuous, sexually dimorphic galls of species-specific morphology on *Eucalyptus* species. In early 1996 we surveyed the species richness and abundance of *Apiomorpha* galls in relation to fire history and species of host eucalypt in mallee vegetation at Danggali Conservation Park, South Australia. Half of the fourteen sites surveyed had been burnt by wildfire in late 1985, whereas the other seven sites had not been burnt for at least 45 years. Only the two commonest of nine *Apiomorpha* species showed little or no host-plant specificity. Long-unburnt sites did not differ in species richness nor in total abundance of *Apiomorpha* galls from sites burnt in 1985, although the two commonest *Apiomorpha* species differed in their responses to fire history. Galls of *A. malleecicola* Gullan were equally abundant at long-unburnt and burnt sites, whereas galls of *A. ovicoloides* (Tepper) were on average four times more abundant at long-unburnt than at burnt sites; this difference may relate to differential dispersal strategies of the first-instar nymphs. We conclude that mallee wildfires at intervals of more than 10 years would be unlikely to impact detrimentally on the long-term survival of a diverse *Apiomorpha* assemblage provided that some long-term unburnt areas (refugia) remain to serve as sources for the colonising nymphs.

KEY WORDS: Fire history, mallee, galls, *Eucalyptus*, Coccoidea, *Apiomorpha*.

Introduction

Fire is a significant factor in Australian ecology and in much of the continent the flora is fire-adapted (Barlow 1981). Many plants, including most *Eucalyptus* L'Hér. species (Myrtaceae), possess fire-protected structures (epicormic buds or lignotubers) from which new growth sprouts, or have seeds that germinate after fires (Gill 1981a,b; Hodgkinson & Griffin 1982; Noble 1982). Such regeneration abilities are particularly characteristic of plants in mallee vegetation, that is, woodland communities dominated by multi-stemmed eucalypts, which are themselves also called mallee (Noble 1982). For many eucalypts, especially mallees, fire can facilitate seed germination (Wellington 1989) or eliminate phytophagous insects (Noble 1982) and parasitic mistletoes (Gill 1981a). Eucalypts dominate most of Australia's forested ecosystems and have complex relationships with native animals, including many insects (Greenstade & New 1991). Habitat management using fire, whether consistent with history (e.g. to recreate purported past Aboriginal land management practice) or for hazard reduction, has effects that are relatively well understood for

vegetation but the implications for many other important organisms, especially invertebrates, are largely unknown (Bradstock *et al.* 1995; Friend & Williams 1996). The few Australian studies of the effects of fire on invertebrates have concentrated on soil and litter-dwelling organisms (e.g. Campbell & Tanton 1981; Neumann & Tolhurst 1991; York 1994) or have sampled a wider invertebrate assemblage using only pitfall traps (e.g. Friend & Williams 1996). Arboreal insects probably survive fires less well than epigeic and hypogeic species (Whelan 1995) and, provided sampling biases can be addressed, should be good candidates for studying the effects of fire on invertebrate populations. In the present study we examine the effects of fire history on endemic Australian scale insects (Hemiptera: Coccoidea) that live only in the canopy of eucalypts.

Scale insects of the genus *Apiomorpha* Rübssamen (Eriococcidae) live within galls that they induce on their eucalypt hosts (Gullan 1984a,b). In *Apiomorpha*, each adult female resides in a large, often symmetrical and woody gall, usually on the stem but sometimes on leaves, buds or fruits of the host eucalypt (Gullan 1984a). These are easily recognised as coecoid galls because there is a small apical orifice through which the female can eliminate her waste honeydew and also mate with the male. Her offspring or first-instar nymphs, called crawlers, make their exit from the maternal gall through this same opening and then disperse to initiate new galls

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on suitable foliage. The galls of males are much smaller than those of the females, rarely more than one centimetre long, and are tubular with an apical orifice and sometimes an outwardly-directed flange at the apex. The shape of the gall of the female is peculiar to the *Apiomorpha* species that induces it, regardless of the identity of the host eucalypt. Most *Apiomorpha* species show some degree of specificity to a restricted range of *Eucalyptus* species (Gullan 1984a). *Apiomorpha* has 39 described species (Gullan 1984a; Gullan & Jones 1989), each of which forms characteristic, sexually-dimorphic galls. Generally, *Apiomorpha* can be identified to species level in the field, even by non-specialists with minimal training.

Scale insects are often claimed to have low vagility (for review, see Hanks & Denno 1993) because the wingless adult females usually spend their entire lives on a single host plant and oviposit there, adult males are short-lived and weak-flying, and all dispersal is due to the movement of the crawlers, which usually remain on their natal host if conditions are favourable (Greathead 1990; Nestel *et al.* 1995). In *Apiomorpha*, our field observations in sclerophyll woodlands have suggested that there is lower diversity and abundance of galls in areas subjected to frequent or severe burning. This reduction seems unrelated to the suitability of post-fire eucalypts for gall development, since the epicormic flush of foliage that follows a fire resembles the preferred plant material utilised by *Apiomorpha* in long-unburnt areas. It is more likely that after a fire kills the galls and their occupants, it takes time for recolonisation by crawlers to occur and if fires are frequent, or potential sources of colonists are distant, local populations may not re-establish. This hypothesis remains speculative in the absence of quantification of any differences in species diversity and abundance between burnt and long-unburnt areas. We investigated re-colonisation after fire by surveying the species richness and abundance of *Apiomorpha* in relation to both the fire history and the species of host eucalypt in mallee vegetation in South Australia.

This study was undertaken in mallee for several reasons. Firstly, mallee is a typically Australian vegetation that has been in serious decline for the past 150 years through land clearance and other forms of degradation (Land Conservation Council 1987; Cheal 1989; Harris 1990). Secondly, it has been hypothesised that mallee plant and animal communities are maintained by episodic fire (Noble 1982, 1989), but no research has been done to investigate how effectively any phytophagous insects re-establish their populations in mallee after fire. Thirdly, it is easier to count the galls on mallee

eucalypts than on the taller forest and woodland species.

Scale insects of *Apiomorpha* are good candidates for studying the effects of wildfire because, unlike more mobile insects (Whelan *et al.* 1980), they are not able to move from their host plants to avoid the flames and, although the thick wall of the galls has been suggested to be an adaptation for fire protection (Koteja 1986), the high intensity of mallee wildfires usually kills the overstorey foliage (Bradstock 1990). In contrast to the well-known biases of pitfalling trapping and other methods of sampling soil or litter fauna (see Whelan 1995), our survey method for *Apiomorpha* potentially assesses the total number of galls on each tree. Further advantages of the use of *Apiomorpha* galls is that their abundance varies little with season of survey since the females of most species probably live for much longer than a year (L.G. Cook unpub.) and galls can remain on the trees for several years after the death of the occupant, thus providing a record of the presence of the species at a site. Lastly, in order to elucidate causal relationships between invertebrate abundance patterns and fire, selected invertebrate groups need to be examined at a finer level of taxonomic resolution than the order or family level that is used in most studies (Friend & Williams 1996). From this perspective, *Apiomorpha* is an ideal study genus because galls can be identified readily to species level, even in the field.

Methods

The work was carried out in Danggali Conservation Park which was established in 1976, became Australia's first Biosphere Reserve in 1977 and is now part of the Bookmark Biosphere Reserve. This quarter of a million hectare reserve is about 90 km north of Renmark in South Australia and lies in the northern half of the Murray basin, adjacent to the New South Wales border (Fig. 1). It includes both arid and mallee land systems and allows access to some spectacular old-growth mallee. Of particular significance to our study is the documented fire history of Danggali Conservation Park (from National Parks and Wildlife Service, South Australia). Fire has not been used as a management tool in the maintenance of its mallee for conservation; recorded wildfires either have been naturally-occurring, following lightning strikes, or the result of human accidents. Many areas have no evidence of burning for a considerable period, perhaps for over a century, or at least not since either 1917 or 1951 when extensive wildfires burnt much of the region. However, of special relevance to the present study is a major lightning-induced fire that burnt a large central area of the reserve in December

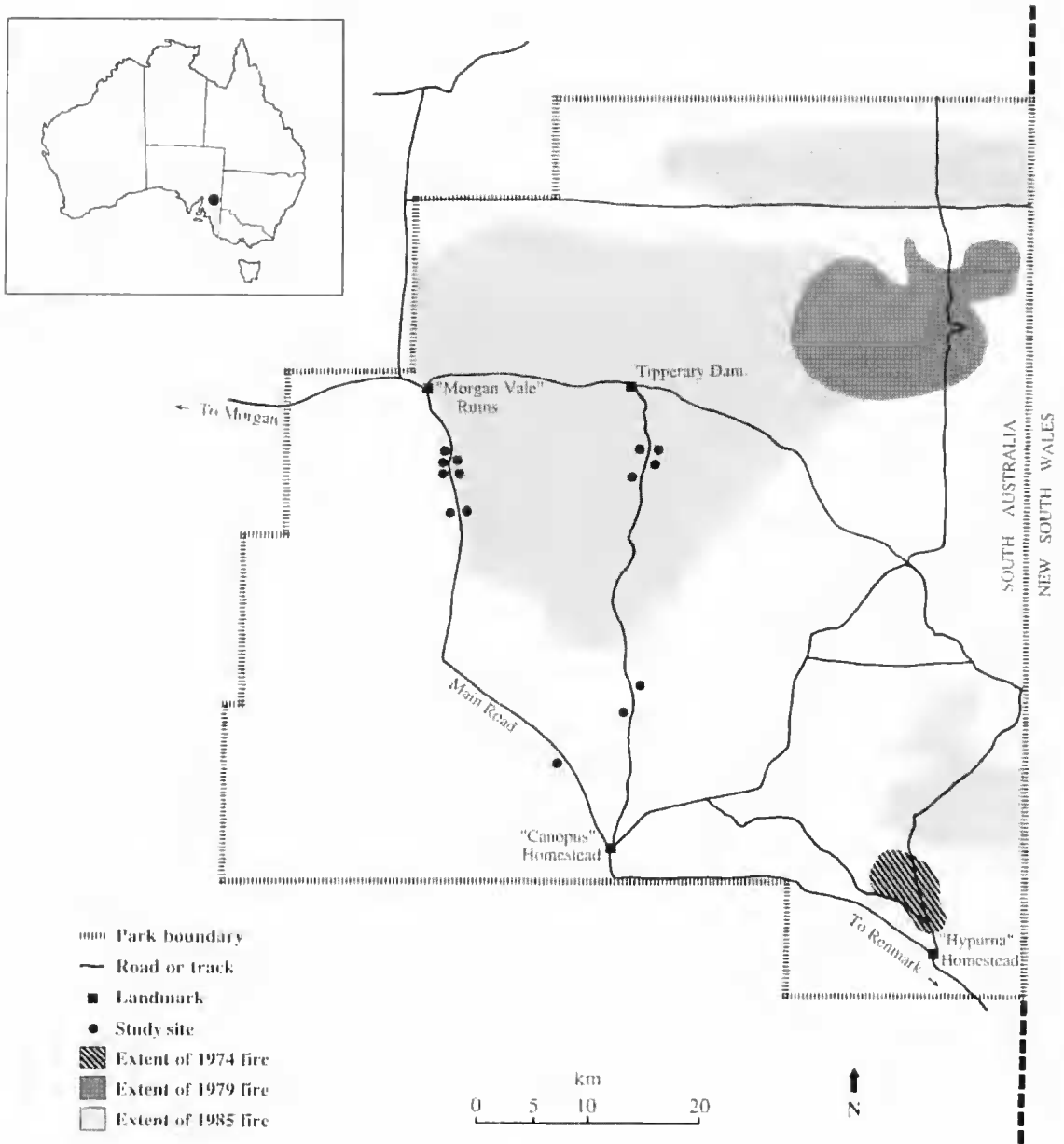


Fig. 1. Map of Danggali Conservation Park, South Australia, showing the extent of recent wildfires and the locations of the 14 study sites where galls of *Apiomorpha* were surveyed. Inset shows location of Danggali Conservation Park. (Figure based on map and aerial photographs from the National Parks and Wildlife Service, South Australia).

1985 (Fig. 1). Since then, the burnt eucalypts have regenerated from their mallee lignotubers, although the dead stags of past substantial limbs still protrude from the now-flourishing mallee regrowth.

We made comparisons between the *Apiomorpha* galls associated with eucalypts in the old-growth mallee ("long-unburnt" sites) and in the mallee that had regenerated after the 1985 fire ("burnt" sites). All fieldwork was conducted in April 1996. Fourteen sites were chosen (Fig. 1), seven in each treatment type (burnt versus long-unburnt), with the site coordinates as given in Table 1. All eucalypts at the burnt sites had been burnt completely in the 1985 fire and sites 6-9 were completely surrounded by post-fire regenerated mallee. We only used burnt sites in the central area of the reserve because we were certain that vegetation in this area had been completely destroyed in 1985, whereas the vegetation around Tipperary Dam and "Morgan Vale" Ruins and in the two smaller areas also burnt in 1985 on the periphery of the reserve (Fig. 1) appeared to have been more patchily burnt. Five burnt and five long-unburnt sites had an understorey with porcupine grass, *Triodia irritans* R. Br. (Gramineae), sometimes as the dominant ground-layer plant. The other four sites either had reasonably bare ground or a mixture of shrub species.

The mallee eucalypt species at the study sites were *Eucalyptus incrassata* Sieber ex DC. (syn. *E. costata* F. Muell. & Behr ex F. Muell.), *E. dumosa* Cunn. ex Oxley, *E. gracilis* F. Muell., *E. oleosa* F. Muell. ex Miq. and *E. socialis* F. Muell. ex Miq. Identification was made using Costermans (1994), except that the name *E. incrassata* (syn. *E. costata*) is retained (M.I. Brooker pers. comm.). The proportions of each species varied according to locality but usually three of the five mallee eucalypts were present at all sites (Table 1). We chose sites in long-unburnt or post-fire regenerating patches to provide 10 multi-stemmed

mallee eucalypts, of between 3 and 6 m in height, per site. These 10 trees were chosen as representative of the proportions of each species in the local area. The height was imposed by the need to inspect the total foliage both from the ground and from a 3 m ladder placed in the centre of the tree.

For each tree we counted the number of galls containing live and dead *Apiomorpha* females. The surveyed galls varied in size from a few mm (young or aborted) to more than 4 cm long, and in shape from cylindrical and bud-like to urn-shaped or ovoid. Galls were recorded as containing dead females if they were old and brown or showed signs of attack by predators or parasitoids. Usually, the presence of a living coecoid was confirmed by the presence of white powdery wax at the gall orifice. Only voucher material and galls of uncertain identity were collected, so the survey was relatively non-destructive. Voucher specimens of galls and slide-mounted insects of *Apiomorpha* have been deposited in the Australian National Insect Collection (ANIC), CSIRO, Canberra.

All data analyses pertain to galls containing live plus dead female insects, unless otherwise stated. The galls of dead insects were included in counts because any successful initiation of a gall was evidence that insect had reached the site and that the tree was a suitable host. Host specificity within *Apiomorpha* was examined by calculating the percentage of the surveyed trees of each eucalypt species that supported galls of females of each *Apiomorpha* species. The response of *Apiomorpha* species to fire was evaluated using one way analysis of variance (ANOVA) to compare burnt and long-unburnt sites in terms of the total numbers of galls of females (of all species summed), total numbers of galls of the seven least common species (i.e. galls of *A. malleacola* Gullan and *A. ovicoides* (Tepper) excluded), and total *Apiomorpha* species found at

TABLE 1. Site localities (from GPS reading) with fire history (long-unburnt (l-u) versus burnt in 1985 (b)) and the number of trees of each species sampled at each site. E. d. = *E. dumosa*, E. g. = *E. gracilis*, E. i. = *E. incrassata*, E. o. = *E. oleosa*, E. s. = *E. socialis*. Numbers at the foot of each species column refer to the total number of trees surveyed for that species.

Site	History	Latitude	Longitude	E. d.	E. g.	E. i.	E. o.	E. s.
1	l-u	33°17'12"	140°35'11"	3	0	3	0	4
2	l-u	33°17'11"	140°35'07"	3	1	0	4	2
3	b	33°17'16"	140°35'02"	0	2	0	6	2
4	b	33°17'00"	140°35'08"	3	3	0	4	0
5	l-u	33°19'20"	140°35'27"	6	0	0	0	4
6	b	33°16'03"	140°43'14"	3	1	1	1	4
7	b	33°16'04"	140°43'08"	6	0	0	0	4
8	b	33°16'34"	140°43'05"	5	1	0	0	3
9	l-u	33°16'50"	140°42'57"	1	5	0	0	4
10	l-u	33°24'36"	140°42'51"	0	5	0	0	5
11	l-u	33°25'02"	140°42'49"	3	4	0	0	3
12	l-u	33°27'19"	140°40'18"	3	2	3	0	2
13	l-u	33°17'04"	140°35'04"	4	4	0	2	0
14	b	33°19'20"	140°35'30"	6	2	0	0	2
				44	35	7	17	39

each site (14 units total). Analysis was carried out at the site level, not the tree level, because there were two or more different tree species per site and many trees had no or few galls. Two species, *A. malleacola* and *A. ovicoloides*, were common enough to examine their individual responses to fire at the site level using ANOVA but the data were transformed [$\ln(x+1)$] to correct for skewness. The responses of *A. malleacola* and *A. ovicoloides* to fire also were evaluated using individual trees as the units of analysis. In this case, binary presences and absences were analysed using Chi Square tests because galls were not abundant or widespread enough to satisfy underlying statistical assumptions at this level. All analyses were carried out using JMP[®] (SAS Institute Inc., © 1989-91).

Results

Apiomorpha species recorded

A total of nine species of *Apiomorpha* was recorded from the sites surveyed. These were: *A. calycina* (Tepper), *A. densispinosa* Gullan, *A. karschi* Rübtsaamen, *A. malleacola*, *A. minuta malleensis* Gullan, *A. ovicoloides*, *A. regularis* (Tepper), *A. strombylosa* (Tepper) and *A. urnalis* (Tepper). All of these species have been collected previously from mallee vegetation in southern Australia (Tepper 1893; Gullan 1984a).

Host-plant specificity of *Apiomorpha*

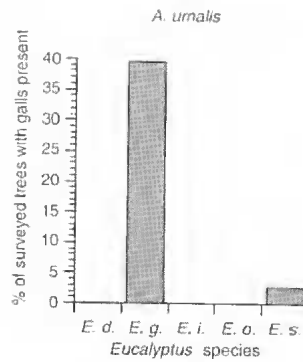
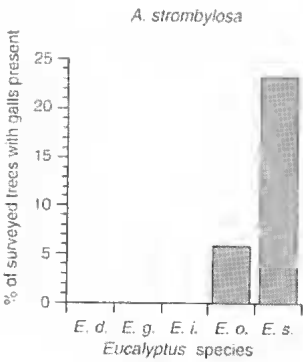
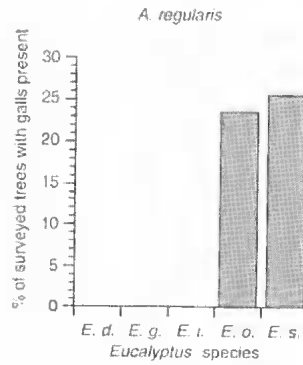
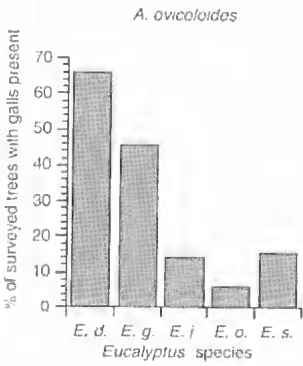
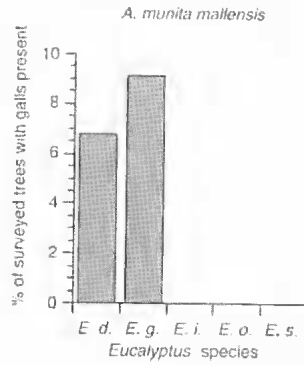
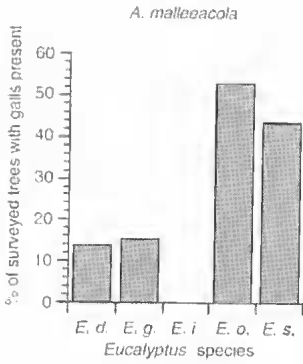
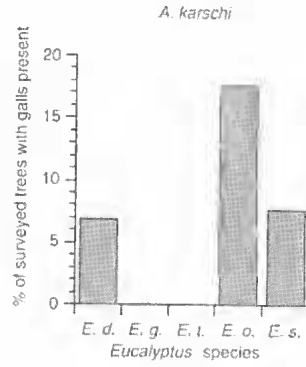
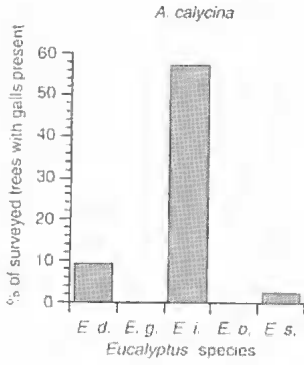
One species, *A. densispinosa*, was recorded from just three sites and solely on *E. dumosa* but only six galls were found and none of these contained a live coecid. Six other of the nine species of *Apiomorpha* showed some degree of host-plant specificity (Fig. 2). Galls of *A. calycina* were found on four of the seven surveyed trees of *E. incrassata* as well as on two other eucalypt species. Galls of *A. karschi* also occurred on three eucalypt species, whereas *A. minuta malleensis*, *A. regularis*, *A. strombylosa* and *A. urnalis* each were recorded from only two eucalypt species. However, 13 of the 14 trees that supported galls of *A. urnalis* belonged to *E. gracilis*, and nine of the 10 trees with galls of *A. strombylosa* were *E. socialis*. Only one species, *A. ovicoloides*, was recorded on all five species of eucalypt; it was the commonest species, occurring on 52 of the 140 surveyed trees. The next most common species was *A. malleacola* which was found on four species of eucalypt and on 37 of the 140 surveyed trees.

Species richness and abundance of *Apiomorpha* in relation to fire history

All nine *Apiomorpha* species were found at both burnt and long-unburnt sites. Burnt and long-unburnt sites did not differ significantly in the number of *Apiomorpha* species recorded on survey trees ($F_{1,12}=3.57$, $p=0.08$) (Table 2). ANOVA of the total

TABLE 2. Means per site \pm 1 SD, or with range in parentheses, and significance of differences due to fire history in diversity of *Apiomorpha* species, number of galls of all *Apiomorpha* species, number of galls of *A. malleacola*, number of galls of *A. ovicoloides* and number of galls of all species excluding *A. malleacola* and *A. ovicoloides*. (For *A. malleacola* and *A. ovicoloides*, means and ranges are from the raw data but F and p values are from transformed data, as indicated by †).

	Long-unburnt	Burnt	F _{1,12} Value	p Value
n (sites)	7	7		
Mean number of <i>Apiomorpha</i> species per site	5.3 \pm 1.1	4.0 \pm 1.4	3.57	0.08
Mean number of <i>Apiomorpha</i> galls per site	37.4 \pm 9.3	24.3 \pm 14.8	3.96	0.07
Mean number of <i>A. malleacola</i> galls per site	6.9 (2-12)	7.6 (0-21)	0.40†	0.54†
Mean number of <i>A. ovicoloides</i> galls per site	13.3 (6-30)	3.4 (0-8)	11.37†	0.01†
Mean number of <i>Apiomorpha</i> galls per site with <i>A. malleacola</i> and <i>A. ovicoloides</i> excluded	16.6 \pm 8.4	12.7 \pm 14.1	0.39	0.54



numbers of galls of females (live and dead) recorded from each site indicated that the fire history of the sites did not affect gall abundances of *Apiomorpha* species ($F_{1,11}=3.96$, $p=0.07$) (Table 2). Burnt and long-unburnt sites did not differ in the percentage of live to dead *Apiomorpha*: 23% of galls at long-unburnt sites and 24% of galls at burnt sites were estimated to contain live cocooids. Except for *A. malleacola* and *A. ovicoloides*, there were insufficient data for statistical analyses based on individual species, although for the third most abundant species, *A. unalis*, there were comparable populations at both burnt and long-unburnt sites.

For *A. malleacola*, ANOVA of the transformed abundance [$\ln(x+1)$] at each site indicated that numbers of galls did not differ between burnt and long-unburnt sites ($F_{1,11}=0.40$, $p=0.54$) (Table 2). Chi Square analyses of presence-absence data for *A. malleacola* on individual trees also indicated that fire history did not affect the likelihood of finding *A. malleacola* galls ($\chi^2_{1,14}=0.04$, $p=0.84$), with galls being present on 27% of all trees sampled in long-unburnt sites and 26% of all trees sampled at burnt sites. If trees of *E. incrassata*, on which *A. malleacola* was never found, were excluded, the results remained very similar ($\chi^2_{1,11}=0.214$, $p=0.64$; galls present on 30% of long-unburnt trees and 26% of burnt trees). Burnt and long-unburnt sites differed only slightly in the percentage of live to dead *A. malleacola*: 33% of galls at long-unburnt sites and 39% of galls at burnt sites were estimated to contain live cocooids. Among the burnt sites surveyed, there was no evidence that galls of *A. malleacola* were more abundant at sites close to (range 1-14 with mean of 6.7 galls per site), compared with distant from (range 0-21 with mean of 8.3 galls per site), long-unburnt areas.

In contrast, for *A. ovicoloides*, ANOVA of the transformed abundance [$\ln(x+1)$] at each site indicated that numbers of galls were significantly lower at burnt sites ($F_{1,12}=11.37$, $p=0.01$) (Table 2). Burnt and long-unburnt sites differed only slightly in the percentage of live to dead *A. ovicoloides*: 19% of galls at long-unburnt sites and 14% of galls at burnt sites were estimated to contain live cocooids. Chi Square analyses of presence-absence data for *A. ovicoloides* on individual trees also indicated that fire history affected the likelihood of finding *A. ovicoloides* galls ($\chi^2_{1,15}=9.04$, $p=0.003$), with galls being present on 49% of all trees sampled in long-unburnt sites, but on only 24% of burnt trees. Among the burnt sites surveyed, galls of *A. ovicoloides* were

slightly more scarce at sites 100-200 m from unburnt vegetation (range 0-3 with mean of 2.0 galls per site) than at sites several km distant from long-unburnt areas (range 1-8 with mean of 4.5 galls per site).

If both *A. malleacola* and *A. ovicoloides* were excluded from the analysis of total numbers of galls, ANOVA of the gall abundance at each site indicated that numbers of galls of the other species combined did not differ between burnt and long-unburnt sites ($F_{1,10}=0.39$, $p=0.54$) (Table 2).

Mortality factors

The original occupants of many of the *Apiomorpha* galls that we recorded during our survey either had been killed by parasitoids, probably wasps, or removed by predators, probably cockatoos and parrots. Some galls had a single, large exit hole in the wall, providing evidence of the emergence of a dart-tailed wasp, *Cameronella* Dalla Torre (Pteromalidae) (Tillyard 1926; Bouček 1988; Naumann 1991), and other galls had many tiny emergence holes. Twelve galls had one side removed which is the typical appearance of a gall opened by a bird. Mortality of the latter kind was twice as common in the long-unburnt sites as in the burnt sites, but there were too few galls damaged in this way to determine whether the difference had statistical significance. Many other galls were brown and obviously dead but generally we could not determine the cause of death. A few other galls were deformed by inquilines, that is, other insects had occupied the gall tissue or the cavity but had not directly killed the *Apiomorpha* female. The identity of the inquilines was not determined because those still occupying the gall were either dipteran or hymenopteran larvae and no rearing to adults was attempted.

Discussion

In the event of fire, season of burn is believed to have the greatest influence on the plant composition of mallee communities, with frequent autumn fires causing substantial mortality of mallee eucalypts (Noble 1982, 1989). Continuous canopy growth of mallee eucalypts can occur after a summer wildfire and may be due to the absence of phytophagous insects (Noble 1982). Fire frequency (the interval between fires) is believed to have the most important long-term effect on mallee fauna because most animals adapt not to fire itself but to the floristic and structural features of the plant communities that result from different fire regimes (Land Conservation

Fig. 2. Host-plant specificity of *Apiomorpha* plotted as the percentage of the surveyed trees of each eucalypt species that supported galls of females of each *Apiomorpha* species; *Eucalyptus* species: *E. d.* = *E. dumosa*, *E. g.* = *E. gracilis*, *E. i.* = *E. incrassata*, *E. v.* = *E. oleosa*, *E. s.* = *E. socialis*.

Council 1987). For invertebrates, which generally exhibit seasonal activity, inappropriate timing and particularly frequency of fire can have damaging consequences for populations (Land Conservation Council 1987; Friend & Williams 1996). For at least some *Triodia* mallee communities, it has been suggested that the natural fire frequency is unlikely to exceed more than one fire every 15–20 years because of the time required for fuel loads to accumulate (Noble 1989). At Dangali Conservation Park, many of the mallee sites that we studied had a *Triodia* understorey and it had been 10.5 years since wildfire had destroyed our burnt sites. Thus, if populations of *Apiomorpha* species in burnt sites could be shown to have recovered to pre-burn levels, the probable natural fire frequency of 15–20 years or more would be unlikely to have any long-term detrimental effects on populations of *Apiomorpha*.

The main findings of our survey were that the long-unburnt sites did not differ in species richness nor in total abundance of *Apiomorpha* galls from sites burnt 10.5 years ago, but that the medium-term effect of fire may vary for different *Apiomorpha* species. For the two species that were common enough to allow analysis of their abundance in relation to fire history, one (*A. malleecola*) was equally abundant in burnt and long-unburnt sites, whereas the other (*A. ovicoides*) was significantly less abundant at the burnt sites. Indeed, for *A. ovicoides*, re-establishment at burnt sites was low even where a source of potential colonists was just across a 10 m wide road. For this species with slow or limited post-fire re-establishment, the effect of another fire in the next five to 10 years might be virtual extinction, especially if no old-growth mallees, that may serve as fire refugia for such insects, survive the fire. The conservation of long-unburnt areas of mallee should be a management priority. Similarly, Friend & Williams (1996) have emphasised the importance of fire management to protect fire-sensitive species and habitats from too-frequent fires in mallee-heath shrublands of south-western Australia.

In contrast, *A. malleecola* and the third most common species, *A. urnalis*, had re-established populations equivalent to those recorded in long-unburnt sites at sites burnt 10.5 years previously (although the number of records for *A. urnalis* were insufficient for statistical analysis). In addition, there were no obvious fire effects on re-establishment of the other six *Apiomorpha* species but numbers of galls observed, at both burnt and long-unburnt sites for each species, generally were low compared with *A. malleecola*. Re-colonisation had occurred at burnt sites that were 10 km or more distant from the nearest stands of long-unburnt mallee. For vagile species, the post-fire flush of growth may be beneficial to gall establishment. This suggestion is

supported by the observation that in other environments, galls of *Apiomorpha* appear to be more abundant on young and regrowth eucalypts than on the foliage of older trees (LeBreton & Vaarwerk 1993; P. J. Gullan pers. obs.). Although this impression may be created by sampling bias (as it is easier to search low foliage of saplings and small trees than the canopy of more mature trees), our glasshouse rearing has shown that the first-instar nymphs will initiate galls only on the new foliage of actively growing shoots. In another study (Yen 1989), the abundance of phytophagous insects, especially sap-sucking species, has been shown to be higher on coppice than mature mallee, perhaps because young leaves and shoots are more nutritious than old foliage and coppice trees have more young growth than mature mallees.

Some *Apiomorpha* species exhibit host-plant preferences for certain eucalypt species. Both *A. regularis* and *A. stramblylosa* occurred only on two eucalypt species, *E. socialis* and *E. oleosa*, which are closely-related species – both are in the series *Subulatae* of *Eucalyptus* (Chippendale 1988). Galls of *A. munita malleensis* were found only on *E. dumosa* and *E. gracilis*, which are in different series (Chippendale 1988). Two very closely-related *Apiomorpha* species, *A. calycina* and *A. urnalis* (Gullan 1984a; L.G. Cook unpub.) showed very different host preferences. Thirteen of the 14 surveyed trees with galls of *A. urnalis* were *E. gracilis*; whereas galls of *A. calycina* were most common on *E. incrassata* and never occurred on *E. gracilis*. Since the two most common *Apiomorpha* species, *A. malleecola* and *A. ovicoides*, also had the broadest host-plant ranges, differences in the occurrence and abundance of these two species in relation to the fire history of sites cannot be attributed to any variation in the composition of eucalypt species among sites. Instead, population differences among *Apiomorpha* species in relation to the fire history of sites may be best explained by differences in their propensity to disperse. The crawlers of some *Apiomorpha* species may disperse more readily to new trees than those of other species. There is ample evidence that first-instar scale insects of other groups are dispersed passively by the wind and, even though mortality is very high, may be carried for distances of a few m to several km, and more rarely a few hundred km, from the natal trees (reviewed by Pedgley 1982; Greathead 1990; Hanks & Denno 1993). Some scale insects crawlers have been reported to orientate downwind and stand on their hind legs with antennae and fore legs outstretched (Washburn & Washburn 1984; Washburn & Frankie 1985; Greathead 1990). Such behaviour probably ensures their dislodgement and dispersal by wind. The crawlers of a few species of

Apiomorpha have been observed displaying similar behaviour under glasshouse conditions (L. G. Cook unpub.). *Apiomorpha* species may differ in their propensity either to disperse actively from the host plant or remain on the natal tree. In contrast to the majority of *Apiomorpha* species, it is extremely difficult to establish infestations of *A. malleicola*, *A. calycina* and *A. unalis* by releasing crawlers on to potted eucalypts in a glasshouse (L. G. Cook unpub.); this suggests that at least some crawlers of the latter species may exhibit obligatory dispersal behaviour and, in the glasshouse, may suicide by actively departing from the only suitable host plant. Under natural conditions, however, natal trees probably would be surrounded by other suitable hosts, especially in mallee vegetation.

Dispersal ability may relate to morphological adaptations as well as behavioural ones. The flattened bodies and two or more long, filamentous caudal setae of scale insect crawlers are believed to enhance their dispersal potential (Wainhouse 1980; Pedgley 1982). Thus differences in body size and shape may partly account for differential dispersal among species. The crawlers of *Apiomorpha* have flattened, oval to subcircular bodies fringed with a continuous row of marginal setae (Gullan 1984a). In addition, the surface area of each marginal seta is extended by a thin sheet of waxy secretion (analogous in general appearance to the vane from the shaft of a feather). The first-instar nymphs of *A. vivicola* are about the same length as, but narrower (195–225 µm at widest part) than, those of *A. malleicola* (265–280 µm wide), although the marginal setae are approximately equal in length (34–44 µm) on both species (L. G. Cook unpub.). If

dispersal ability in *Apiomorpha* is correlated with the surface area of the body of the crawlers, the differences in abundances of *A. malleicola* and *A. vivicola* in burnt and long-unburnt sites may be attributed at least in part to differences in the size and shape of their crawlers.

Selection for both active dispersal behaviour and body morphology that favours passive drift may occur in scale insect species that occupy unpredictable or temporary habitats, as has been suggested for armoured scale insects that feed on short-lived versus long-lived host plants (Greathead 1990). If this hypothesis is valid for *Apiomorpha*, then some species, such as *A. malleicola*, can be postulated to be better adapted to the vagaries of fire in the mallee environment.

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